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Sexual Conflict and the Evolution of Female Preferences for Indicators of Male Quality

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ABSTRACT: Males and females have opposing interests when it comes to the honesty of signals used in mate choice. The existence of this sexual conflict has long been acknowledged, but its consequences have not been fully investigated. By applying adaptive dynamics methods and individual-based computer simulations to a standard model for good-genes sexual selection, we show that sexual conflict over condition-dependent signaling can prevent the handicap process from ever attaining an evolutionary equilibrium. We outline the parameter conditions and properties of the underlying genetics conducive to nonequilibrium behavior and discuss the potential of such behavior to explain the elaboration and frequent phylogenetic loss of sexually selected traits. We also evaluate its consequences for well-established insights of sexual selection theory previously shown to apply when female mating preference and male ornament expression do converge on stable equilibrium levels. Contrary to equilibrium expectation, a continual change of condition-dependent signaling enables the evolution of a costly preference for a pure epistatic indicator and the evolution of preferences for redundant signals or a large number of independent ornaments. We thus conclude that seemingly general results of sexual selection theory, insofar as these are based on equilibrium considerations, do not extend to cases where nonequilibrium behavior occurs.

Keywords: nonequilibrium dynamics, multiple ornaments, adaptive dynamics, revealing handicap, condition-dependent handicap.

Why do females so often show mating preferences for elaborate male ornaments that evidently reduce the male's viability? This question touches on one of the central issues in sexual selection theory, and it has led to the development of several theories for the evolution of female mating preferences (Andersson 1994). One widely held view (reviewed in Maynard Smith 1991) is that female choice based on costly male traits is adaptive because the male ornaments, on which female preference acts, serve as indicators of good genes.

There exists a conflict between the sexes over the reliability of such indicators. Whereas female interests are served by ornaments that reliably signal the genetic quality of the male, it is in the interest of males to undermine the association between the good genes and the expression of the ornament as far as possible such that males that do not carry the good genes are also able to attract females. In view of this conflict, it has long been realized that the signaling function of the ornament must be induced by genetic or physiological processes that cannot easily be modified without large costs (potential mechanisms are discussed in, e.g., Clutton-Brock 1982; Hamilton and Zuk 1982; Møller 1990; Andersson 1994). In such a case, the male ornament handicaps male survival in such a way that cheating (i.e., expressing the ornament without carrying the good genes) is costly (Zahavi 1975).

To capture the essence of this idea, early theoretical models of the handicap process (e.g., Maynard Smith 1985; Pomiankowski 1987; Andersson 1994 and references therein) assume that the genetic and physiological architecture of the ornament dictates a fixed pattern of condition-dependent ornament expression. By doing so, the early models successfully provide proof of principle that the handicap process can work. However, by imposing a fixed relation between quality and ornament expression, these models eliminate the sexual conflict over the reliability of the ornament as an indicator of good genes, and they do not address the issue of the maintenance of condition-dependent signaling in a situation where males can adapt their investment into the ornament in relation to their own genetic quality.

As an important next step, Grafen (1990), Iwasa et al. (1991), and Iwasa and Pomiankowski (1994) therefore investigated the evolution of optimal patterns of condition-

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dependent investment into the ornament. Two conclusions can be drawn from their analyses. First, an optimal pattern of condition-dependent investment maximizes the fitness of males, irrespective of their quality, and not that of females. In particular, low-quality males will increase their investment into the ornament as long as this increases their reproductive success. This makes it more difficult for females to distinguish high-quality from low-quality males. Hence, the expression of the ornament by low-quality males compromises the signaling function of the ornament and the fitness of females. Second, condition-dependent signaling will be maintained only when the ornament is either a condition-dependent or a revealing handicap. By definition (e.g., Iwasa et al. 1991), an ornament is a condition-dependent indicator when it is more costly to produce for low-quality males. An ornament is a revealing indicator if its state reflects the condition of the male such that the attractiveness of low-quality males is lower than that of high-quality males, even if they invest equally into the ornament. In both cases, the optimal level of investment is lower for low-quality males, either because the cost of ornament expression increases more rapidly for such males (condition-dependent handicap) or because the benefit in terms of mating success increases more slowly (revealing handicap).

It is by no means guaranteed that an optimal pattern of condition-dependent ornament expression will actually be realized in the course of evolution. Evolutionary stability (sensu Maynard Smith and Price 1973) and attainability are independent properties (Geritz et al. 1998), and, paradoxically, evolution may lead away from an evolutionarily stable strategy (ESS; Abrams et al. 1993). Optimality considerations (Grafen 1990; Iwasa et al. 1991) should therefore be complemented by a stability analysis based on evolutionary rates and dynamics. The relevance of this point for sexual selection theory was illustrated by Iwasa and Pomiankowski (1995), who observed evolutionary cycling of mating characters in a Fisherian sexual selection model. The instability of Fisher's (1930) runaway process underlying such continual evolution arises for certain (genetic) parameter values when the survival cost of the male ornament is small around the viability selection optimum and rapidly increasing beyond a certain level of exaggeration. Although this particular instability is not likely to affect handicap evolution—unless the variation in male quality is small and the handicap process is not very effective (Iwasa and Pomiankowski 1995, 1999)—it is conceivable that other mechanisms could destabilize the evolutionary equilibria of good-genes sexual selection. The coevolutionary dynamics of condition dependence and mating preference could well be such a mechanism, given that more examples of continual coevolution between the sexes driven by sexual conflict have been described (e.g., Rice 1996; Gavrilets 2000).

Iwasa and Pomiankowski (1994) were the first to study the dynamics of condition dependence in good-genes sexual selection. Their analysis concerns cases where the evolutionary rate of change of the female mating preference is small relative to that of the male condition-dependent signaling strategy. Under that restriction, the evolution of condition dependence will actually converge on the equilibrium predicted by ESS analysis (Iwasa and Pomiankowski 1994), as can also be observed in various simulation studies (e.g., Iwasa and Pomiankowski 1999; Houle and Kondrashov 2002; Lorch et al. 2003). Houle and Kondrashov (2002), however, also show a simulation for different parameter values where the evolutionary outcome deviates from what one would expect from optimality considerations. In this simulation, the female mating preference evolves at a relatively high rate. This apparently destabilizes the feedback between the strategies of the two sexes and results in continual evolutionary change in mating preference and ornament expression.

The sexual conflict inherent to the handicap process is currently not fully understood, and the factors that determine whether the evolution of mate choice and condition-dependent signaling will settle on stable equilibrium levels have not yet been systematically characterized. For that reason, a first objective of this article is to study in detail the dynamics of condition dependence in good-genes sexual selection. Our analysis will include selective factors, such as the costs of choice or the reliability of the ornament as a signal for quality, as well as genetic details, such as the magnitude of mutational variances and covariances. Both may qualitatively affect the attainability of evolutionary equilibria (Matessi and Di Pasquale 1996).

A second objective of this article is to explore the consequences of continual evolution in condition-dependent signaling for some of the seemingly general insights offered by theory on the evolution of mating preferences for good-gene indicators. An example of such an insight is the conclusion that no stable exaggeration of costly female preference is possible when the ornament is a pure epistatic indicator (Iwasa et al. 1991; Maynard Smith 1991). Another example is the conclusion that females should evolve preferences for the single indicator of quality with the highest reliability, honesty, and detectability and should disregard ornaments that are inferior in these aspects (Schluter and Price 1993). These insights are based on the results of equilibrium analyses of the handicap process and are therefore expected to apply when the evolutionary dynamics converges on a stable equilibrium. Whether they also apply when the handicap process does not attain equilibrium remains to be seen.

An Overview of the Model and Some Methodological Remarks

To investigate the combined action of good-genes sexual selection and sexual conflict over condition-dependent signaling, we analyze a formal model of the handicap process with flexible male condition-dependent ornament expression (as in Iwasa and Pomiankowski 1994). We study the evolution of four quantitative traits: genetic quality, female mating preference for an ornament, and investment into the ornament by high- and low-quality males. The genetic quality of an individual affects its viability. Moreover, it influences the costs of ornamentation and/or male attractiveness: the male ornament is a condition-dependent or a revealing handicap. Female fitness depends on genetic quality and the cost of choice. Male fitness depends on genetic quality, the cost of ornament production, and male mating success. The latter is determined—through mate choice—by the preferences of females and the realized size of the ornament.

We deviate from existing models in one aspect. Instead of using a quantitative genetics framework (reviewed in Mead and Arnold 2004) or an ESS analysis (e.g., Pen and Weissing 2000), we use adaptive dynamics theory (Metz et al. 1992; Dieckmann and Law 1996; Geritz et al. 1998; Hofbauer and Sigmund 1998) to analyze the evolutionary dynamics. This allows us to obtain explicit expressions for the fitness gradients without having to consider the intricate dependence of genetic variances and covariances on the parameters of the model, as is necessary in quantitative genetic models. Moreover, for the purpose of this study, estimating equilibrium values of the genetic variances and covariances as functions of the model parameters (Pomiankowski and Iwasa 1993) would not be sufficient. We would have to keep track of their dynamics as well. Although this is feasible (Barton and Turelli 1991), the procedure to do so is quite complicated and involves restrictive assumptions.

The adaptive dynamics method describes evolution as a mutation-limited process. This approximation simplifies the analysis of our model, but when applied to genetic quality, it does not allow for the presence of variation in this character. Because the handicap process relies on such variation, we explicitly model deleterious mutations in genetic quality. For the female preference and male sexual characters, the assumption of mutation-limited evolution has the consequence that we cannot address the effects of genetic covariances between preferences and male characters. Such covariances are instrumental in driving Fisher's runaway process of sexual selection (Fisher 1930). Our analysis is therefore restricted to cases where the impact of Fisher's process on the evolutionary dynamics is weak relative to that of the handicap process. The complementary regime, which has been analyzed by Iwasa and Pomiankowski (1999), is realized when males show low variance in quality or when the effect of quality differences on viability is small such that the handicap process is not effective. Provided that the handicap process can work effectively, our mutation-limited model of good-genes sexual selection captures the essence of evolution in polymorphic populations with small genetic variation, as demonstrated by the good quantitative agreement between the predictions of the analytical model and individual-based computer simulations (see below; cf. van Doorn and Weissing 2004), which do not impose restrictions on the magnitude of genetic covariances or the amount of genetic variation present in the population.

The Model

Genetic Quality

We initially assume that an individual's genetic quality can be represented as a one-dimensional quantity. Genetic quality is determined by an arbitrary number of diploid loci, with two alleles at each locus (denoted **A** and **a**). The allele **A** confers a higher quality; the allele **a** confers a lower quality. Variation at the quality loci is maintained through biased deleterious mutations, which convert **A** alleles into **a** alleles. Deleterious mutations occur with probability μ per genome per generation.

To keep the model analytically tractable, we assume that the rate of beneficial mutations, which convert a low-quality to a high-quality allele, can be neglected relative to the rate of deleterious mutations and that μ is itself small such that we may neglect the frequency of individuals that carry more than one low-quality allele. Under these simplifying assumptions, we need to keep track of the frequencies of two different types of individuals: individuals that carry only high-quality alleles (phenotype A) and individuals that carry a deleterious mutation at one of their quality loci (phenotype a). Throughout this article, the index k will be used to refer to these quality phenotypes (i.e., $k = A$ or a).

Viability Selection

We assume that generations are discrete and nonoverlapping. Viability selection acts at the start of every generation, before reproduction. Individual survival probabilities vary with the individual's general (i.e., good-genes-induced) viability, which is determined by the individual's genetic quality. The general viabilities associated with the different quality phenotypes are defined by the parameters v_k, where $v_A > v_a$.

Survival probabilities are also affected by the costs associated with the expression of preferences (for females) or ornaments (for males). These factors are assumed to interact multiplicatively with general viability. The cost of choice varies with female preference p. Females with larger absolute values of p exert stronger mating preferences (see below); females with $p = 0$ mate at random, which, by assumption, minimizes the costs of choice. Specifically, we take the survival probability for females with quality phenotype k, $v_k^f(p)$, as

$$v_k^f(p) = v_k v^f(p) = v_k \exp(-\gamma p^2), \tag{1}$$

where the function $v^f(p) = \exp(-\gamma p^2)$ measures the cost of choice and the parameter γ determines how rapidly viability decreases with the strength of preference.

For males with quality phenotype k, the survival probability is given by $v_k^m(t_k)$, where

$$v_k^m(t_k) = v_k \exp(-\beta_k t_k^2). \tag{2}$$

The second factor on the right-hand side incorporates the cost of ornament production. It varies with t_k, the male's investment of resources into the ornament. The phenotypic characters t_k are expressed relative to the value optimal for male survival (also implying that negative values of t_k are biologically meaningful) such that $t_k = 0$ is the optimal investment into the ornament when only viability selection is considered. As implied by the index k, male investment into the ornament is condition dependent; that is, males may invest more or less resources into the ornament, depending on their genetic quality. In addition to this indirect dependence of viability on genetic quality, we allow for the possibility that the male's genetic quality directly influences the cost of ornament production, as is commonly assumed in condition-dependent handicap models. The parameters β_k determine the intensity of stabilizing selection on the investment of resources into the ornament. In general, $\beta_a \geq \beta_A$, but when the ornament is a condition-dependent handicap, $\beta_a > \beta_A$. The viability of low-quality males is then more severely compromised by ornament expression than is that of high-quality males, even when both types of males would invest equally into the ornament.

Mate Choice

For the sake of concreteness, let us suppose that females evaluate males based on the realized size, $S_k(t_k)$, of their ornament. Ornament size is again expressed relative to the value optimal for male survival. Males that invest more into their ornament will produce a larger ornament. Hence, $S_k(t_k)$ is an increasing function of t_k. In addition, we allow for the possibility that the realized size of an ornament is directly affected by the quality of the male, as is commonly assumed in revealing handicap models.

Before she mates, a female evaluates the available males based on the size of their ornaments and her own preferences. Females have a higher probability of mating with an attractive male, where attractiveness is quantified by a function r_k. The attractiveness of a male with quality phenotype k is proportional to

$$r_k(p, t_k) = \exp[pS_k(t_k)]. \tag{3}$$

In this mate choice model, also known as the psychophysical or open-ended model of mate preference (Lande 1981), positive values of p indicate preferences for larger ornaments, negative values of p indicate preferences for smaller ornaments, and females with $p = 0$ mate at random. A female mates only once. The probability that a given male is allowed to father her offspring is determined by the male's attractiveness relative to the average attractiveness of the other males present in the population.

For all males, the realized size of an ornament is proportional to the investment into that ornament. Yet, if the ornament is a revealing indicator of quality, low-quality males must invest more to attain the same level of ornament elaboration and, hence, attractiveness. Therefore, we assume that

$$S_k(t_k) = t_k \alpha_k. \tag{4}$$

The parameters α_k reflect how efficiently male investment into the ornament translates into a larger (more attractive) ornament for a male with quality phenotype k. All else being equal, high-quality males are more attractive than low-quality males or, at the very least, are equally attractive. Hence, $\alpha_A \geq \alpha_a$.

Information Content

The values of the parameters α_k and β_k depend on a variety of biological factors, such as female perception, the physiology of male ornament production, and the ecological setting of mate choice. From the male's point of view, these parameters determine the attractiveness gain and survival cost of trait investment for low- and high-quality males, respectively. They therefore determine how easily a male can produce an elaborate ornament without actually carrying high-quality alleles. From the female's point of view, the parameters α_k and β_k determine how easily a female can discriminate between high- and low-quality males. To characterize ornaments in this respect, we will use the term "information content"; we will say that an ornament has high information content if a low level of preference is sufficient to accurately distinguish high-quality from low-quality males and low information content if females have to evolve high levels of preference to do so.

The information content of an ornament is determined by two factors. First, it depends on the constraints on male condition-dependent signaling that arise from the genetic and physiological architecture of the male ornament. Such constraints are captured by the parameters α_k and β_k, which therefore directly determine what one could call the intrinsic information content of the ornament. For example, when $\alpha_A > \alpha_a$ and $\beta_A = \beta_a$, the ornament intrinsically provides information about genetic quality through a revealing handicap mechanism; when $\alpha_A = \alpha_a$ and $\beta_A < \beta_a$, it does so through a condition-dependent handicap mechanism; and finally, when $\alpha_A > \alpha_a$ and $\beta_A < \beta_a$, the ornament is a revealing and a condition-dependent handicap at the same time. In contrast, the ornament does not intrinsically provide information about genetic quality when $\alpha_A = \alpha_a$ and $\beta_A = \beta_a$ (in this case, the ornament is a pure epistatic indicator; Maynard Smith 1991). We emphasize that our use of the terms "revealing handicap," "condition-dependent handicap," and "epistatic indicator" always refers to the intrinsic information content of the ornament and not necessarily to its realized information content.

Indeed, the realized information content of the ornament could be different from its intrinsic information content, as a result of the condition-dependent signaling strategy of males. The distribution of the male strategic variables t_k thus constitutes a second factor to impinge on the information content. For example, if the ornament is a pure epistatic indicator, it may still convey information about genetic quality if, for some reason, low-quality males invest less into the ornament than high-quality males. Alternatively, if the ornament is a revealing handicap, it may still provide no information whatsoever about quality if low-quality males invest more into the ornament than high-quality males such that they compensate exactly for their reduced attractiveness.

In these two examples, the realized information content of the ornament is larger or smaller, respectively, than its intrinsic information content. It is clear that further evolution will take place whenever such discrepancies exist. For example, if the realized information content is higher than the intrinsic information content of the ornament, low-quality males could easily increase their mating success by evolving stronger expression of the ornament. In the opposite case, low-quality males experience relatively high costs of signaling, and they are expected to reduce their investment into the ornament. Intuitively, one would expect the realized information content of an ornament to agree with its intrinsic information content in evolutionary equilibrium. Indeed, in the following section, we demonstrate how this intuition can be formalized. This does not imply, however, that such an equilibrium will ever be attained in the course of evolution. This issue will be addressed in "Evolutionary Dynamics and the Stability of Equilibria."

Evolutionary Equilibria

We study the long-term evolution of the female mating preference and the pattern of condition-dependent ornament expression in males by considering evolution as a sequence of mutation and allele substitution events. Following the standard assumptions of adaptive dynamics theory (e.g., Geritz et al. 1998), we assume that the genes coding for the female preference and investment into the ornament by males mutate only rarely. This allows us to focus on a population with negligible variation for these traits. We then consider an initially rare mutant allele that causes individuals to differ slightly in one of their phenotypic components from the resident individuals, and we investigate whether this mutant allele will be able to increase in frequency. Mathematically, the potential for the mutant allele to spread is determined by the mutant's invasion fitness λ, that is, by the long-term geometric rate of increase of the mutant allele frequency in the context set by the current resident alleles (Metz et al. 1992). The mutant will spread if its geometric rate of increase is positive, that is, when its invasion fitness is larger than that of the resident allele.

The fitness difference between mutant and resident alleles is approximated by the gradient of the invasion fitness function. Hence, this gradient determines the direction of evolutionary change. If the selection gradient is positive, subsequent mutation and trait substitution events will lead to an increase of the trait under consideration (and vice versa if it is negative).

General Properties of Evolutionary Equilibria

A derivation of the invasion fitness function and its gradients with respect to the different evolutionary characters is given in appendix A in the online edition of the *American Naturalist.* Only the end result of this derivation is given here. The selection gradients with respect to the male characters, denoted λ_{t_k}, are given by

$$\lambda_{t_k} = \frac{\partial \lambda}{\partial t_k} = b_k \frac{\partial \ln [r_k(p, t_k) v_k^m(t_k)]}{\partial t_k}, \tag{5}$$

where the coefficients b_k are strictly positive (see app. A).

Under suitable assumptions, evolution proceeds in a direction correlated with the direction of the selection gradient (Dieckmann and Law 1996; Weissing 1996; Hofbauer and Sigmund 1998). Potential endpoints of evolution are therefore points where the selection gradient vanishes (i.e., points where $\lambda_{t_k} = 0$). In view of equation (5), male condition-dependent investment into the ornament will therefore evolve to maximize $r_k(p, t_k)v_m^k(t_k)$, the product of male attractiveness and male survival for each male quality phenotype. Under quite general assumptions on the functions r_k and v_k^m, this implies that in equilibrium, low-quality males will invest less resources into the ornament because the cost of ornamentation increases more rapidly for such males (condition-dependent handicap), because attractiveness increases less rapidly (revealing handicap), or because both of these mechanisms act at the same time.

A similar intuitive interpretation can be given for λ_p, the selection gradient with respect to female preference. In appendix A, we derive that

$$\lambda_p = \frac{\partial \lambda}{\partial p} = \frac{1}{2}\frac{\partial \ln [v^f(p)]}{\partial p} + \frac{1}{2}\mu w \frac{\partial \ln [R(p, t_A, t_a)]}{\partial p}, \qquad (6)$$

where w is the reproductive value of males that carry a low-quality allele and the function R measures the attractiveness of high-quality males relative to that of males carrying a deleterious mutation; that is,

$$R(p, t_A, t_a) = \frac{r_A(p, t_A)}{r_a(p, t_a)}. \qquad (7)$$

According to equation (6), female preference will evolve away from its viability selection optimum (i.e., to a point where $\partial \ln [v^f(p)]/\partial p$ is negative) only if mutation bias creates variation among males ($\mu > 0$) and $\partial \ln (R)/\partial p$ is larger than 0 (for the moment, we suppose, without loss of generality, that p, t_A, and t_a are positive).

The latter term has an interesting biological interpretation. For females that mate at random, low-quality males are, by definition, as attractive as high-quality males. To females that exhibit stronger preferences, however, high-quality males will appear increasingly attractive because such males invest more into their ornament (this is to be expected when the ornament is a condition-dependent handicap) or because the ornament is a revealing indicator. Therefore, R is a monotonically increasing function of p. The term $\partial \ln (R)/\partial p$ represents the rate at which the relative attractiveness of high-quality males increases with female preference, and it reflects the detectability of quality differences. It is related to the realized information content of the ornament, which we define as the detectability of quality differences relative to the level of choosiness, that is, $1/p \cdot \partial \ln (R)/\partial p$.

If $\partial \ln (R)/\partial p$ is only slightly larger than 0, the relative attractiveness of high-quality males increases only slowly with preference, even when female preference is already high. Therefore, females must evolve high levels of choosiness before they can accurately distinguish high-quality from low-quality males. In this situation, the realized information content of the ornament is low, meaning that the ornament is a poor indicator for genetic quality. On the other hand, when $\partial \ln (R)/\partial p$ is large, even low levels of choosiness will allow females to select high-quality males. In this case, the ornament has a high realized information content.

Evolutionary Equilibria for Our Specific Model

After these general considerations, we now return to the specific model defined earlier. Hence, we substitute specific functions for r_k, v_k^m, and v^f, as defined in equations (1)–(4). This immediately yields simple expressions for the equilibrium investment of resources into the ornament by males, t_A^* and t_a^*:

$$t_k^* = p^* \frac{\alpha_k}{2\beta_k}. \qquad (8)$$

Depending on whether the ornament is a revealing indicator or a condition-dependent handicap, either α_k is smaller or β_k is larger for low-quality males. For both types of handicaps and at equilibrium, low-quality males will therefore invest less into their ornaments.

The equilibrium female preference, p^*, cannot be obtained in a simple explicit form. From equation (6), it follows that

$$-\frac{\partial \ln [v^f(p^*)]}{\partial p^*} = \mu w^* \frac{\partial \ln [R(p^*, t_A^*, t_a^*)]}{\partial p^*}, \qquad (9)$$

which implies that

$$2\gamma p^* = \mu w^* p^* \left\{ \frac{1}{p^*} \frac{\partial \ln [R(p^*, t_A^*, t_a^*)]}{\partial p^*} \right\}. \qquad (10)$$

As indicated by the asterisk, the reproductive value w^* is a function of p^* (see app. A). The factor between fences on the right-hand side is the realized information content of the ornament in equilibrium. When it is 0, there can be no stable costly mate preference (in this case, the only equilibrium solution is $p^* = 0$).

We now use equations (7) and (8) to find that the realized information content of the ornament in equilibrium equals

$$\begin{aligned}\frac{1}{p^*}\frac{\partial \ln[R(p^*, t_A^*, t_a^*)]}{\partial p^*} &= \frac{1}{p^*}(\alpha_A t_A^* - \alpha_a t_a^*)\\ &= \frac{\alpha_A^2}{2\beta_A} - \frac{\alpha_a^2}{2\beta_a}. \qquad (11)\end{aligned}$$

We interpret the constant on the right-hand side as the intrinsic information content of the ornament because it depends only on the inherent characteristics of the ornament that are represented by the parameters α_k and β_k and not on the male signaling strategy. Equation (11) corroborates the intuition that the realized information content of an ornament (on the left-hand side) should equal its intrinsic information content (on the right-hand side) in evolutionary equilibrium. When the ornament is a revealing handicap ($\alpha_A > \alpha_a$), a condition-dependent handicap ($\beta_A < \beta_a$), or both at the same time, the intrinsic information content of the ornament is strictly positive. Contrastingly, when $\alpha_A = \alpha_a$ and $\beta_A = \beta_a$, the ornament is a pure epistatic indicator, and its intrinsic information content is 0.

From equations (8) and (10), it is easy to see that there always exists a trivial equilibrium $p^* = t_k^* = 0$ at which females mate at random. In addition, there exists a pair of nontrivial equilibria ($p^* = \pm\tilde{p}$, $\tilde{p} > 0$) where females choose males with costly ornaments when

$$2\gamma < \mu\frac{\alpha_A^2/(2\beta_A) - \alpha_a^2/(2\beta_a)}{2(v_A/v_a) - 1}, \qquad (12)$$

that is, when the intensity of sexual selection for increased choosiness outweighs the intensity of stabilizing viability selection on female preference.

Evolutionary Dynamics and the Stability of Equilibria

In the previous section, we identified evolutionary equilibria by searching for points at which the selection gradients vanish. To determine whether evolution will actually proceed toward these equilibria, we must determine the stability properties of the equilibria. This requires us to be more specific about the actual evolutionary dynamics of the female preference and the male investment pattern.

The evolutionary dynamics of traits is determined not only by the direction of the selection gradient but also by genetic factors (Matessi and Di Pasquale 1996; Weissing 1996). In quantitative genetics models, for example, these genetic factors are incorporated by a genetic variance-covariance matrix, which determines how easily selection can lead to an evolutionary response in a specific phenotypic direction. In adaptive dynamics models, the genetic variance-covariance matrix does not play a role because evolution is assumed to be mutation limited. Instead, adaptive dynamics models have to deal with genetic constraints imposed by the mutation process. For example, evolution may preferentially proceed in certain phenotypic directions because of the fact that mutations are more likely to result in phenotypic deviations in these directions. Alternatively, selection on one trait may lead to a correlated response in another because of the fact that mutations of the one trait have pleiotropic effects on the other.

Indeed, following Dieckmann and Law (1996), the evolutionary rate of change in the female preference p and the male investment strategy t_k is given by

$$\frac{d}{d\tau}\begin{bmatrix} p \\ t_A \\ t_a \end{bmatrix} = \rho\mathbf{G}\begin{bmatrix} \lambda_p \\ \lambda_{t_A} \\ \lambda_{t_a} \end{bmatrix}, \qquad (13)$$

where the matrix **G** is the mutational variance-covariance matrix, which contains as elements the mutational variances and covariances of the different traits. The proportionality constant ρ scales the rate of evolution with the rate at which beneficial mutations arise (ρ depends on the population size and the mutation rate; Dieckmann and Law 1996). Finally, τ represents evolutionary time. A unit of evolutionary time roughly corresponds to the generation time if mutation creates, on average, a single new mutant phenotype per generation in the entire population; it is of the order of one-tenth of the generation time, when mutation creates on average 10 new mutant phenotypes per generation, and so on.

Mutations with Pleiotropic Effects

In view of equation (13), the attainability, or convergence stability, of equilibria depends on the direction of selection in the vicinity of the equilibrium. An equilibrium is bound to be convergence stable when the selection gradients point toward the equilibrium from whatever direction it is approached (Leimar 2001). However, if this is not the case, convergence stability may be qualitatively affected by the underlying genetics (Matessi and Di Pasquale 1996). This implies that an equilibrium may be attained only if the mutational variance-covariance matrix satisfies certain conditions.

As illustrated in figure 1, this is especially relevant for our model. The figure shows two numerical simulations of the dynamical system (13) (see eq. [B1] in app. B in the online edition of the *American Naturalist*) that differ only with respect to the mutational variance-covariance matrix **G**. For the sake of concreteness, we supposed that the female preference p and the male investment strategies t_k are encoded by a large number of genes and that a fraction f of the male investment genes is expressed irrespective of the genetic quality of the male. Hence, a

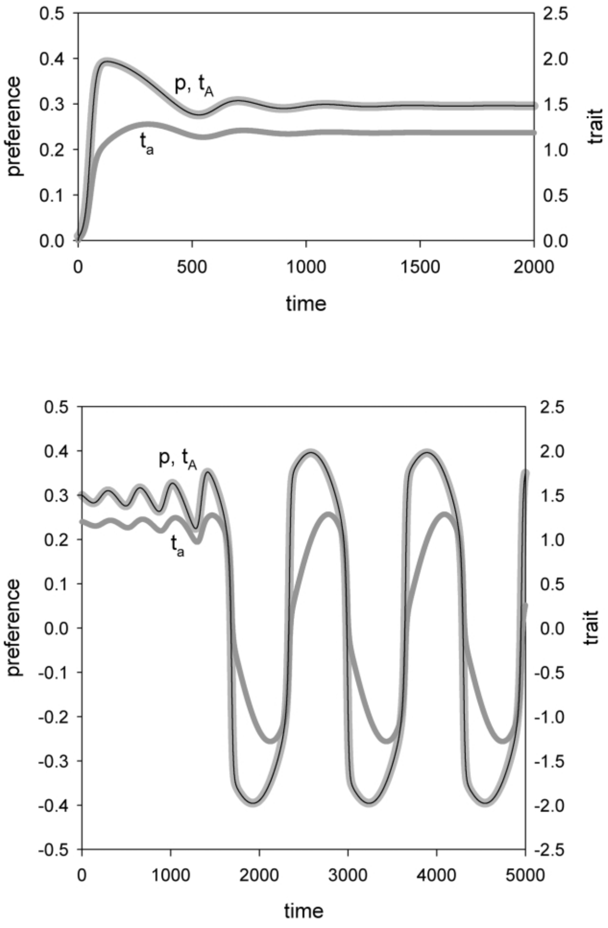

Figure 1: Genetic details influence the stability of equilibria. *Top*, female preference and male investment into the ornament reach a stable equilibrium where females are choosy and where males develop costly ornamentation. The equilibrium loses its stability when the pleiotropic effects of mutations in male investment genes are decreased. *Bottom*, simulation starts from initial conditions close to the equilibrium. Female preference and male investment levels diverge from the equilibrium until they eventually attain a stable limit cycle. Parameters are $\alpha_A = 5.0$, $\alpha_a = 4.0$, $\beta_A = \beta_a = 0.5$, $\gamma = 0.05$, $\mu = 0.05$, $v_A = 1.0$, and $v_a = 0.5$.

mutation in one of these genes has pleiotropic effects on the characters t_A and t_a simultaneously. These pleiotropic effects enter the matrix **G** as mutational covariances (app. B).

If the mutational covariance between the male investment genes is large enough, evolution converges on a stable nontrivial equilibrium, as in figure 1 (*top*), where $f = 0.4$. In equilibrium, a stable level of female preference is attained, and also the male investment pattern reaches a stable state where $t_a = 4/5t_A$ (this is because $\alpha_a = 4/5\alpha_A$ and $\beta_a = \beta_A$; cf. eq. [8]). However, when we decrease the overlap between the male ornament genes, the equilibrium loses its stability (fig. 1, *bottom*; $f = 0.3$). Instead of attaining stable equilibrium values, the female preference and the investment into the ornament by males now continue to fluctuate and eventually approach a stable limit cycle. This limit cycle is projected in figure 2 (*black curve*), together with some illustrative trajectories (*gray*) that connect the different equilibria to one another and to the limit cycle. In this figure, p and t_A are both represented on the horizontal axis. This is possible because t_A is always close to its quasiequilibrium value (eq. [8]) and, hence, proportional to p (see also fig. 1, where the lines representing p and t_A are virtually overlapping).

The continual evolution of the female mating preference and the male condition-dependent investment pattern along the limit cycle is driven by a sexual conflict over the information content of the ornament. Such a conflict can arise when there is a potentially large discrepancy between the realized and intrinsic information contents of the ornament. Indeed, in the simulations shown in figures 1 and 2, we assumed that the ornament was a revealing indicator with a low intrinsic information content. This does not necessarily imply, however, that females can never use the

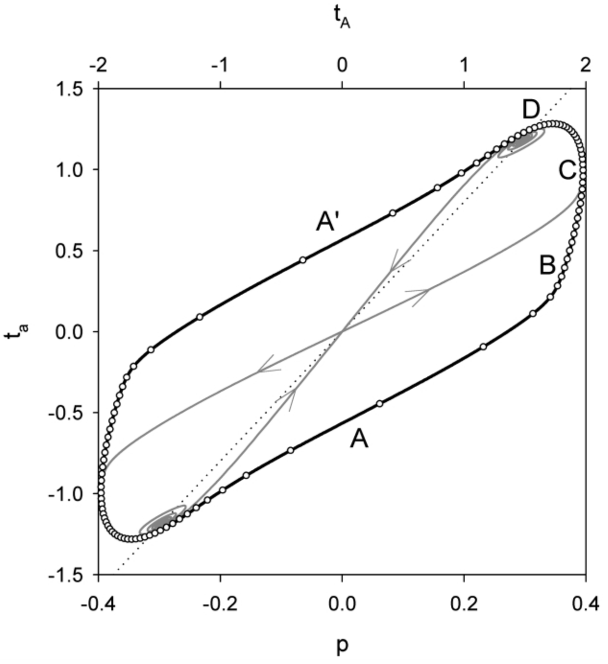

Figure 2: Continual evolution along a limit cycle. Sexual conflict over the information content of the ornament drives the female preference and the male investment strategy along a limit cycle (*black curve*). White circles are plotted at regular time intervals to give an indication of the rate of evolution along the cycle. Gray trajectories connect the trivial and nontrivial equilibria to one another and to the limit cycle. The dotted line marks the optimal investment of resources into the ornament by low-quality males for any given level of female preference. Parameters are as in figure 1.

ornament to gain accurate information about genetic quality. Imagine, for example, that female preference is weak and that for some reason $t_a < t_A$, as is the case at point *A* in figure 2. In this situation, females benefit from evolving preference because females can very easily discriminate between high- and low-quality males based on the ornament. This is not so much because the ornament intrinsically provides a lot of information about quality but rather because of the pattern of condition-dependent investment that is currently adopted by the male population.

In view of the high realized information content of the ornament, it is not surprising that females rapidly evolve preference for the ornament up to the level where the benefit of choice is balanced by the cost (fig. 2, point *B*). Along with the increase of female choosiness, males increase their investment into the ornament, as one would predict based on equation (8). Because the ornament is an indicator that reveals only limited information about quality ($\alpha_a = 4/5\alpha_A$ and $\beta_a = \beta_A$), one would expect this to lead to a situation where $t_a = 4/5t_A$, as in figure 1 (*top*). Although this situation is eventually attained (fig. 2, point *D*; the dotted line is to indicate all points where $t_a = 4/5t_A$), it is approached only slowly. Apparently, the male character t_a evolves at a very low rate. This has an important consequence: for a long time, the ornament continues to function as an indicator with a high realized information content, even though its intrinsic information content is low.

There are two reasons for the low rate of evolution of the male character t_a. First, t_a is expressed only in low-quality males. The frequency of such males is of the order of the mutation rate μ such that t_a is hardly exposed to selection. Second, selection on the other male characters only weakly affects t_a (through pleiotropic mutations) because the overlap between male investment genes is low ($f = 0.3$ in fig. 2).

Even though the male character t_a approaches its optimal value only slowly, low-quality males will inevitably catch up with the high-quality males. The realized information content of the ornament will therefore eventually decrease to match the intrinsic information content (fig. 2, point *D*). Initially (fig. 2, between points *B* and *C*), females respond to the gradual erosion of the realized information content of the ornament by evolving stronger preferences. By doing so, females can continue to distinguish between high- and low-quality males, even though the difference between these males has become smaller (cf. Hill 1994). Eventually, this strategy turns out to be fruitless. Evolving stronger preferences yields higher costs of choice, whereas it cannot prevent the benefit of choice from gradually being eroded further. In the end, females have evolved strong preferences for an ornament that now provides only rather limited information about genetic quality. The costs of choice are no longer balanced by the benefits, and the female preference collapses (fig. 2, point *C*).

The decrease of female preference is immediately tracked by a reduction of the investment by high-quality males. Low-quality males again respond much more slowly. Beyond point *D* in figure 2, low-quality males invest even more resources into their ornament than high-quality males. This provides an additional selection pressure for the females to lower their preference for the ornament until it is lost completely (fig. 2, point *A'*). From this point onward, the whole process repeats itself in the other direction.

Individual-Based Computer Simulations

Formally, our deterministic mathematical model (summarized by eq. [13]) offers an exact description of the evolutionary dynamics of the female preference p and the male investment strategies t_k only under highly idealized circumstances (e.g., evolution must be mutation limited, and inheritance of the evolving characters should be based on additive haploid genetics). To investigate to what extent the dynamics defined by equation (13) is representative for the outcome of evolution under less idealized conditions, we implemented our model as a genetically explicit, stochastic, individual-based simulation program (app. B). Individual-based simulations can potentially deal with arbitrarily complex genetics and do not impose restrictions on the magnitude of genetic covariances or the amount of genetic variation present in the population.

Figure 3 shows data from an individual-based simulation run (*solid lines*). We used the same model parameters as in figures 1 and 2, except that t_A and t_a were assumed to be coded by nonoverlapping sets of genes; that is, $f = 0$. As in the deterministic version of the model, the individual-based simulations show a continual evolution of the female mating preference and the male investment strategy along a limit cycle. This illustrates that the occurrence of nonequilibrium dynamics does not critically rely on the simplifying assumptions underlying our mathematical analysis.

Beyond the mere qualitative agreement, the two versions of the model actually generate quantitatively comparable predictions for the evolutionary trajectories. Both the amplitude and the period of the oscillations observed in the individual-based simulation match well with the predictions from the deterministic model. This is clearly observable in figure 3, where the dashed lines show numerical solutions of equation (13) for exactly the parameter conditions used in the individual-based simulations (app. B).

The fit between the individual-based simulation results and the predictions based on the deterministic model deteriorates when the effects of stochasticity become more

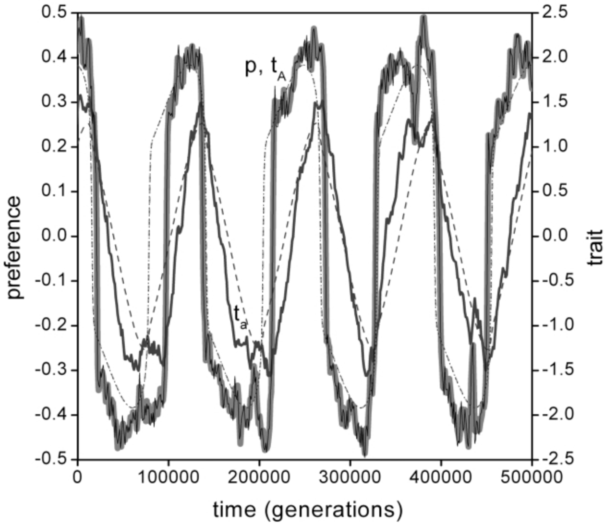

Figure 3: Continual evolution in an individual-based simulation. The evolutionary dynamics of the female preference and male investment strategy was investigated by means of an individual-based simulation program (app. B in the online edition of the *American Naturalist*). Solid lines show the evolution of the population averages of p, t_A, and t_a through time (the population size in the simulation was set at 5,000 individuals). As in the deterministic model, the lines representing the averages of p and t_A are virtually overlapping. Dashed lines show numerical solutions of the deterministic model (eq. [13]). The parameter conditions that were used in the individual-based simulations (see fig. 1; $f = 0$) were also used in the deterministic model. Also, the mutational variance-covariance matrix **G** and the proportionality constant ρ that appear in equation (13) were a priori derived from the parameters of the individual-based simulations (app. B).

pronounced. For example, individual-based simulations for smaller population sizes do show oscillatory behavior, but the period of the evolutionary cycles is less regular. This observation highlights the considerable effect that stochasticity could have on the evolutionary response to sexual selection, but it does not lead us to doubt the general robustness of the conclusions based on the mutation-limited deterministic approach. Because the latter is much more accessible to further analysis than an approach based on individual-based simulations, we will concentrate on the deterministic version of our model (eq. [13]) from here on.

An Exploration of Different Parameter Conditions

Because of the large number of parameters, it is hard to characterize the behavior of the model under a wide range of conditions. We therefore reduced the number of parameters by rescaling the model (app. B). By doing so, we were able to identify dimensionless combinations of parameters that govern the model's behavior.

In figure 4*A*, we systematically varied two of these dimensionless parameter combinations. Along the vertical axis, we varied c, the relative cost of choice; along the horizontal axis, we varied V, the typical rate of evolution of the male characters relative to that of the female preference.

These dimensionless parameters are defined as follows:

$$c = \frac{4\gamma\beta_A}{\mu\alpha_A^2},$$

$$V = \frac{\mathrm{Var}\,(t_A)}{\mathrm{Var}\,(p)}\frac{4\beta_A^2}{\alpha_A^2}. \tag{14}$$

The relative cost of choice c measures the intensity of viability selection on female preference, which is quantified by 2γ, relative to that of sexual selection, which is quantified by $\mu\alpha_A^2/(2\beta_A)$. The coefficients $\mathrm{Var}\,(t_A)$ and $\mathrm{Var}\,(p)$ that appear in the definition of V are the mutational variances of the male character t_A and the female preference, respectively. When $\mathrm{Var}\,(t_A) \gg \mathrm{Var}\,(p)$ such that V is large, comparable intensities of selection on t_A and p lead to a much larger phenotypic change in the male character per generation and, hence, to a larger rate of evolution of this character. Contrastingly, when V is small, mutation is more likely to create variation in female preference such that the evolutionary rate of change of p is larger than that of t_A, provided, of course, that both characters experience selection of comparable intensity.

Roughly speaking, the dynamics of the model can be one of four qualitatively different types. As illustrated in figure 4*A*, all of these types may occur when V and c are varied. The figure is subdivided into four large regions (regions 1–4), and the dynamics of the model within a region is represented by the schematic phase portraits (cf. fig. 2) shown within that region. The regions are separated by boundary lines, which correspond to combinations of V and c where a qualitative change occurs in the stability or the number of equilibria (local bifurcation lines; *black*) or where limit cycles appear or disappear through global bifurcations (*gray lines*).

In region 1 of figure 4*A*, where V is large and c is small, the dynamics is as in figure 1 (*top*); that is, evolution converges on a stable nontrivial equilibrium where females are choosy and where males develop a costly ornament. The equilibrium is destabilized when the relative rate of male evolution V is decreased. We then enter region 2, where the female preference and the male investment strategy evolve continuously along a limit cycle, as in figures 1 (*bottom*) and 2. The mechanism responsible for the appearance of oscillations is a classical one: by decreasing the relative rate of male evolution, we lower the rate at

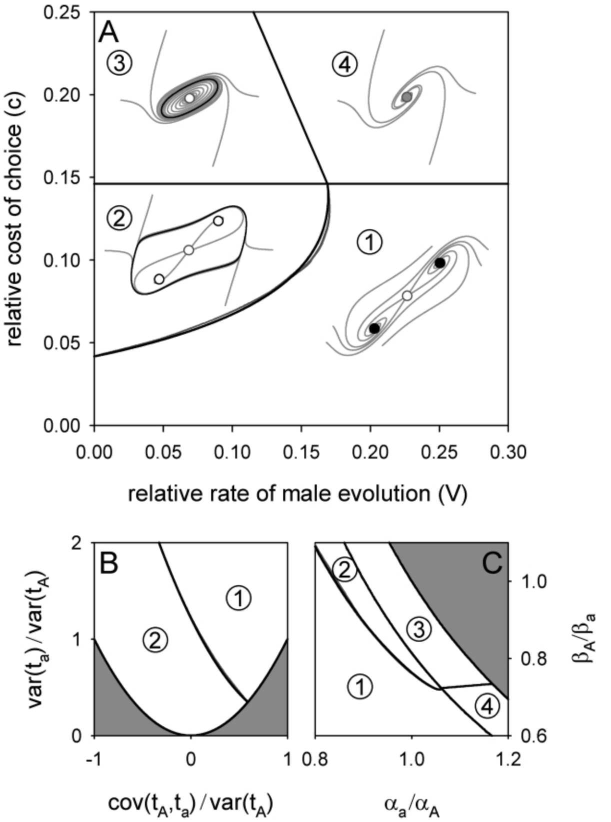

Figure 4: Model behavior under different parameter conditions. The dynamics of the model can be one of four types (see the main text), which each occur within a specific region (1–4) of parameter space. In *A–C*, we vary different combinations of parameters. Black lines demarcate points where the number or stability of equilibria changes through local bifurcations; gray lines (often very close to local bifurcation lines) demarcate points where limit cycles appear or disappear through global bifurcations. Gray areas extend over biologically unrealistic parameter combinations. The dynamics within each region is characterized by a representative phase portrait (as in fig. 2). In these phase portraits, black lines indicate stable limit cycles, and circles mark equilibrium points (gray is used for the trivial equilibrium, black for the nontrivial equilibrium; filled circles indicate stable equilibria; open symbols indicate unstable equilibria). Except when a parameter combination was varied, we used the values $\alpha_a/\alpha_A = \beta_A/\beta_a = 0.9$, $v_a/v_A = 0.7$, $c = 0.1$, $V = 0.15$, $\mu = 0.01$, $\mathrm{Var}(t_a)/\mathrm{Var}(t_A) = 1.0$, and $\mathrm{Cov}(t_A, t_a)/\mathrm{Var}(t_A) = 0.1$.

which males respond to changes in the female preference. This effectively introduces a delay in the feedback between the evolution of female preference and male condition-dependent investment (it is well known from engineering that systems with delayed feedbacks are prone to exhibit oscillatory behavior).

Changes in the relative cost of choice predominantly influence the number of equilibria. Figure 4*A* illustrates that the nontrivial equilibria (i.e., the equilibria at which females exert costly mate preference) disappear as soon as the relative cost of choice becomes larger than a certain threshold value (cf. eq. [12]). Hence, we find convergence to the trivial equilibrium (i.e., the equilibrium where females mate at random and where males do not express a costly ornament) in region 4 and oscillations around the trivial equilibrium in region 3. The model's behavior in region 3 illustrates again that predictions based on equilibrium considerations can be misleading: although the cost of choice is high relative to the intrinsic information content of the ornament and although one would therefore not expect females to evolve mating preferences, it is obvious that the cost of choice is not minimized in region 3. Because of the continual change of mating preferences, the realized information content of the ornament is above its intrinsic information content for most of the time. As a consequence, the average benefit of choice is larger than one would expect from equilibrium considerations. This also explains why female choosiness can evolve when the relative costs of choice are higher than the threshold level determined by equation (12).

The same four types of dynamical behavior are found when other parameters are varied (the labeling of the regions in fig. 4*B* and 4*C* corresponds to the labeling used in fig. 4*A*). In figure 4*B*, for example, we vary the relative genetic covariance between the male characters (on the horizontal axis) and their mutational variances relative to one another (on the vertical axis). The gray background extends over biologically unrealistic parameter combinations (app. B). From figure 4*B*, we conclude that continual evolution of the female preference and the male investment pattern is likely when the male characters evolve independently ($\mathrm{Cov}(t_A, t_a) = 0$) or when mutations typically affect the male characters in opposite phenotypic directions ($\mathrm{Cov}(t_A, t_a) < 0$). This agrees with the results shown in figure 1, where a decrease of the mutational covariance between male characters (the parameter *f*) gave rise to oscillatory dynamics. Likewise, continual evolution is more likely when the mutational variance of the character t_a is low such that this character can evolve only slowly. Again, this will destabilize the evolutionary feedback through introducing a longer delay in the evolutionary response by low-quality males.

Figure 4*C*, finally, features the same configuration of regions and bifurcation lines as figure 4*A*. In figure 4*C*, we vary the intrinsic information content of the ornament. Along the horizontal axis, we vary the relative coefficients of attractiveness ($\alpha_a/\alpha_A < 1$ for a revealing handicap). Along the vertical axis, we vary the relative coefficients for the cost of ornamentation ($\beta_A/\beta_a < 1$ for a condition-dependent handicap). The gray region extends over irrelevant parameter combinations. At the border of the gray region, the ornament is a pure epistatic indicator that does not intrinsically provide information about quality. The intrinsic information content of the ornament increases as one moves downward or toward the left in the plot. The potential discrepancy between the realized and intrinsic information content of the ornament, which is responsible for the observed evolutionary cycling of the female preference and the male investment strategy, can be large only when the intrinsic information content of the ornament is low. Otherwise, deviations from the optimal male investment pattern would be too costly to persist over a long time. This agrees with figure 4*C*, where continual evolution of female preferences (regions 2 and 3) is restricted to the area in parameter space where the intrinsic information content of the ornament is low. In the remaining areas, equilibrium analysis correctly predicts the outcome of evolution. In addition, we can draw the conclusion that both revealing and condition-dependent models may exhibit oscillatory behavior.

Multiple Viability Components, Multiple Ornaments

In this section, we investigate two extensions of our model in order to illustrate some of the potential consequences of sexual conflict over the information content of signals in more complex settings.

Multiple Viability Components

Our first extension concerns our assumption that genetic quality can be represented as a one-dimensional quantity. Although this is a standard assumption, made in many models of sexual selection on good genes (for exceptions, see Johnstone 1996; van Doorn and Weissing 2004), it is usually the case that genetic quality has several independent aspects (e.g., Doucet and Montgomerie 2003).

To explore the consequences of this complication, we extend our model by introducing a second set of quality genes that influence genetic quality. To be precise, we assume that genetic quality is determined by two distinct quality components (instead of one), denoted A and B. These quality components represent, for example, tolerance to harmful substances in the environment and resistance against parasites. Each of the quality components is determined by many loci with two alleles (**A** and **a** for the first quality component; **B** and **b** for the second). As in the original model, we assume that deleterious mutations maintain variation in both quality components but that they are sufficiently rare such that we may neglect the frequency of individuals that carry more than one deleterious mutation. Under these assumptions, we must keep track of the frequencies of three types of individuals: high-quality individuals that carry no deleterious mutations (*AB* individuals), low-quality individuals that carry an **a** allele (*aB* individuals), and low-quality individuals that carry a **b** allele (*Ab* individuals). Males can vary their investment into the ornament depending on their quality for each of the quality components. The levels of investment by the three types of males are denoted t_{AB}, t_{aB}, and t_{Ab}.

A derivation of the invasion fitness and the selection gradients for this extended model follows a procedure similar to the one given in appendix A for our original model (details are available from the authors). The main difference between the extended and the original model is that the selection gradient with respect to the female preference now contains two separate contributions to the benefit of choice, one for each quality component. To be exact (cf. eq. [6]),

$$\lambda_p = \frac{1}{2}\frac{\partial \ln [v^f(p)]}{\partial p} + \frac{1}{2}\mu_A w_A \frac{\partial \ln [R_A(p, t_{AB}, t_{aB})]}{\partial p} + \frac{1}{2}\mu_B w_B \frac{\partial \ln [R_B(p, t_{AB}, t_{Ab})]}{\partial p}, \qquad (15)$$

where μ_K denotes the rate of deleterious mutations in quality component K ($K = A$ or B), w_K is the reproductive value of a males with a low quality for component K, and R_K denotes the attractiveness of a high-quality male relative to that of a male with a low quality for component K.

In a model with multiple quality components, it is possible that the ornament is a signal with a high intrinsic information content for one component of quality and a low intrinsic information content for another. In such a situation, there is a potentially large discrepancy between the intrinsic and the realized information content of the ornament with respect to one of the quality components. As in the original model, this may lead to continual evolution of female mating preferences along a limit cycle.

Even more complex behavior emerges when the ornament has a low intrinsic information content for both quality components. The realized information content of the ornament can then differ from its intrinsic information content in both aspects of quality. Much like the motion of a double pendulum, this may result in a fundamentally unpredictable dynamics of the female preference and the male investment strategy. An example of this is given in figure 5, where we show the evolution of female preference for a pure epistatic indicator and the male investment strategy in a model where male quality is determined by two independent quality components.

Multiple Ornaments

The second extension of our model deals with the evolution of multiple preferences and ornaments (reviewed by Candolin [2003]). Male courtship displays often comprise multiple sexual signals, involving several behavioral

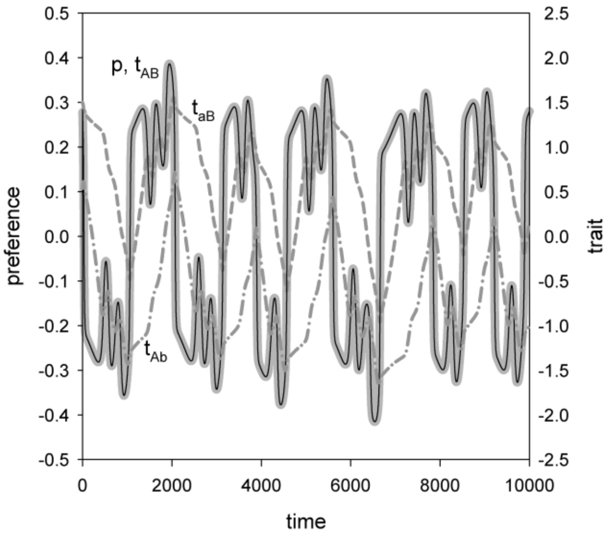

Figure 5: Complex dynamics of an indicator for two distinct aspects of quality. The advantage of evolving a preference varies with the investment into the ornament by low-quality males (*dashed line* = males with low quality for the first component; *dot-dashed line* = males with low-quality for the second component). For each quality component separately, the benefit of choice decreases when the realized information content of the ornament drops. For the ornament as a whole, the information content varies in a complex manner because of the fact that it serves as an indicator for two quality components at the same time. Much like the chaotic movement of a double pendulum, this results in an unpredictable dynamics of the female preference. Parameters are $\alpha_{AB} = \alpha_{aB} = \alpha_{Ab} = 5.0$, $\beta_{AB} = \beta_{aB} = \beta_{Ab} = 0.5$, $\gamma = 0.05$, $\mu_A = \mu_B = 0.025$, $v_{AB} = 1.0$, and $v_{aB} = v_{Ab} = 0.5$. Mutations in a male investment character had no pleiotropic effects on other characters.

attributes and/or morphological ornaments. The reasons for this complexity are poorly understood. Theoretical models indicate that the evolution of multiple preferences is not straightforward. At first sight, females are expected to evolve preference for the single indicator of quality with the highest reliability, honesty, and detectability (Schluter and Price 1993; Iwasa and Pomiankowski 1994), and they should disregard ornaments that are less reliable, honest, or detectable. This is especially true when there are epistatic interactions between the costs of the different female preferences such that the overall cost of choice is greatly increased when females assess an additional male trait (Iwasa and Pomiankowski 1994). We investigated one solution to this problem and demonstrated that preferences for multiple ornaments can evolve, even when exhibiting multiple preferences is costly, as long as the ornaments provide information about different aspects of genetic quality or when they provide sufficiently independent estimates of overall genetic quality (van Doorn and Weissing 2004). In this article, we provide a second solution to the problem: the nonequilibrium dynamics of preferences and male investment may lead to the establishment of multiple preferences even in situations where this is impossible in evolutionary equilibrium.

An example of such a situation is given in figure 6. The figure shows the evolution of two female preferences for two male ornaments that both act as signals of genetic quality (for details, see app. B). As in our original model, genetic quality was assumed to be a one-dimensional quantity. Hence, the ornaments did not act as signals for distinct quality components, nor did they provide independent estimates of genetic quality. What is more is that the costs of choice were taken to combine in a supermultiplicative manner such that the use of a second preference greatly increased the cost of mate choice. A careless extrapolation of existing theory (Schluter and Price 1993; Iwasa and Pomiankowski 1994; van Doorn and Weissing 2004) would therefore lead us to predict the evolution of, at most, a single female preference. Yet, figure 6 clearly demonstrates this prediction to be wrong.

In the simulation shown in figure 6, the parameters of the first ornament are identical to those of the ornament

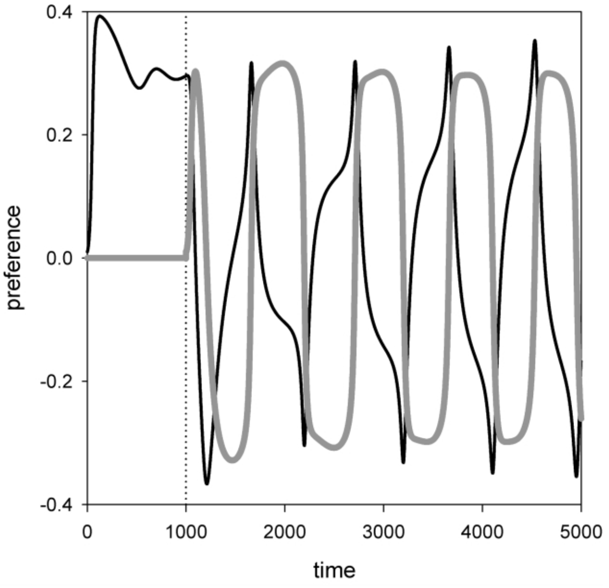

Figure 6: Preferences for two truly redundant signals. The figure shows the evolution of two female preferences in a species with two male ornaments. In the first 1,000 time units, female preference for the first ornament (*black line*) reaches a stable equilibrium level (exactly as in fig. 1, *top*). After 1,000 time units, we introduce a small level of preference for a second ornament. Although the second ornament has a lower intrinsic information content, female preference for the second ornament (*gray line*) can increase. Both female preferences remain in the population. Again, the system eventually attains a stable limit cycle. Parameters are as in figure 1, *top*. The additional parameters for the second ornament (see app. B in the online edition of the *American Naturalist*) are given by $\alpha'_A = 7.0$, $\alpha'_a = 6.0$, $\beta'_A = \beta'_a = 0.5$, and $\gamma' = 0.08$.

in figure 1. For the first 1,000 time units, the simulation therefore behaves exactly as the simulation shown in figure 1 (*top*): female preference for the first ornament (*black line*) and male investment into that ornament (not shown) approach a stable equilibrium level. After 1,000 time units, we perturbed the system slightly by introducing a small preference for the second ornament (*gray line*). The second ornament is an ornament with a low intrinsic information content. Females evolve a preference for this ornament even though it is an inferior indicator of quality and even though using multiple preferences is costly. The establishment of the second ornament induces a continual change in the relative information contents of the two ornaments. This allows for the dynamical maintenance of both preferences, notwithstanding the fact that existing theory precludes the stable maintenance of both preferences in an evolutionary equilibrium.

The dynamical maintenance of a large number of ornaments and preferences can be illustrated even more convincingly when the two extended versions of our original model are combined and generalized (app. B). A combined model, where genetic quality is determined by several distinct quality components and where female mate choice is based on an arbitrary number of ornaments and preferences, allows for the maintenance of many ornaments and preferences even when the number of quality components is low. We observed the joint evolution of up to 20 ornaments and preferences in a model with just two quality components, a result that bears analogy to the dynamical coexistence of a large number of competing species on just a few resources (Huisman and Weissing 1999). For the sake of clarity, a less dramatic example of a simulation is provided as figure B1 in the online edition of the *American Naturalist*.

Discussion

Existing theory on the evolution of mating preferences for good-gene indicators concentrates on cases where female preference and male ornament expression eventually attain an evolutionary equilibrium. Yet, convergence on a stable equilibrium, as observed by, for example, Iwasa and Pomiankowski (1999), Houle and Kondrashov (2002), and Lorch et al. (2003), is not the only possible outcome of the handicap process. Alternative dynamical outcomes include an evolutionary runaway for an increasingly strong handicap trait (Iwasa and Pomiankowski 1994) and evolutionary cycling (Iwasa and Pomiankowski 1999; Houle and Kondrashov 2002). In this article, we investigated sexual conflict over the information content of the signals used in mate choice as a potential source of instabilities in the handicap process. Our results indicate that the feedback between male condition-dependent signaling and female mate choice strategies can easily be destabilized, preventing the handicap process from ever reaching equilibrium.

Well-established insights of sexual selection theory that apply under equilibrium conditions need not necessarily hold when the handicap process does not attain equilibrium. For example, although the stable exaggeration of a costly female preference for a pure epistatic indicator (or a sufficiently unreliable condition-dependent or revealing handicap) is precluded under equilibrium conditions (Iwasa et al. 1991), nonequilibrium dynamics may still allow for the long-term dynamical persistence of such a preference (fig. 4, area *A*; fig. 5). A similar word of caution applies to the insight that females should evolve preferences for the single indicator of quality with the highest reliability, honesty, and detectability and should disregard ornaments that are inferior in these aspects (Schluter and Price 1993), at least unless using an additional cue in mate choice only weakly increases the cost of choice (Iwasa and Pomiankowski 1994) or unless the ornaments provide independent information about distinct aspects of quality (van Doorn and Weissing 2004). Indeed, figure 6 shows the joint evolution of preferences for two ornaments in a situation where the careless extrapolation of equilibrium considerations would lead us to predict that females should use only a single preference.

The oscillations of mate preference and male ornament expression observed in our model superficially resemble those observed in Fisherian models of sexual selection (Iwasa and Pomiankowski 1995). Yet, the mechanism underlying the oscillations is quite different in the two types of models. The instability of Fisher's process affects handicap evolution only when the handicap process acts weakly (Iwasa and Pomiankowski 1999). The instability is mediated by the genetic covariance between preference and male trait expression, an evolutionary factor that, by assumption, does not affect the dynamics in our model. Instead, the present analysis concerns a complementary regime where the impact of Fisher's process on the evolutionary dynamics is small relative to that of good-genes sexual selection. In our model, instabilities are generated by the handicap process itself, through the coevolution of condition dependence and mating preference. Interestingly, both the Fisherian and the good-genes model illustrate the importance of genetic constraints on the evolutionary dynamics of secondary sexual characters. In both these models, the stability of equilibria depends partially on genetic details that affect the relative rates of evolution. This illustrates that a purely phenotypic approach to the modeling of sexual selection, without the appreciation of genetic details, is inappropriate.

Apart from its theoretical consequences, the continual evolution observed in our model is interesting in its own right. Wiens (2001) mentions the feedback between female preference and male signaling as a possible explanation for the apparent frequent turnover and loss of sexually selected traits, arguing that female preference for an ornament (and, hence, the corresponding ornament itself) will disappear as soon as males manage to express their ornaments regardless of their genetic quality. As illustrated by figure B1, the evolution of multiple ornaments and preferences can indeed lead to expression patterns of sexual characters that are highly variable and dynamic on the phylogenetic timescale. In addition, the model provides an alternative mechanism for divergence of sexually selected traits between allopatric populations (Schluter and Price 1993). This may be of relevance in the context of speciation. Third, the model captures some aspects of the ideas originally developed by Hill (1994), who suggests sexual conflict in the evolution of quality indicators to be responsible for the elaboration of male signals from their initial rudimentary form to larger or more complex manifestations of the ornament. According to this idea, females are forced to assess additional and novel ornament features in order to still be able to estimate the quality of the male whenever the information content of male advertisement decreases. This may result in an evolutionary race, where a correlation between male ornament expression and male genetic quality can be maintained only through the establishment of increasingly complex female mating preferences and increasingly elaborate male ornaments (Hill 1994).

When Should We Expect Nonequilibrium Dynamics of Preferences and Indicator Traits?

The question of whether the continual evolution of preferences and good-gene indicators is a biologically relevant evolutionary phenomenon ultimately remains an empirical one. On the basis of our analysis, we can, however, give a number of conditions under which sexual conflict over the information content of ornaments is most likely to affect the evolutionary dynamics.

First, males should be able to change their investment into the ornament according to their genetic quality. Instabilities leading to continual evolution are more likely when the investment strategies of high- and low-quality males can evolve independently or when the genetic architecture of the ornament tends to enlarge the differences between high- and low-quality males (fig. 4*B*). Different assumptions on the genetic basis of condition dependence will lead to a different mutational (co)variance structure, and we surmise that such differences can explain why evolutionary cycling has been observed in some models (Houle and Kondrashov 2002) but not in others (Iwasa and Pomiankowski 1994; Lorch et al. 2003). Second, discrepancies between the realized and intrinsic information content of the ornament should not be too costly. This requires that the ornament is a poor indicator of quality and that the intrinsic information content of the ornament is low (fig. 4*C*). In this case, females cannot easily detect low-quality males. Also, males that invest less than the optimal value do not suffer disproportionately from reduced attractiveness. Consequently, there can be a discrepancy between the realized and the intrinsic content of the ornament without this resulting in strong selection on males to realize their optimal level of investment. Third, discrepancies between the realized and intrinsic information content of the ornament should persist for sufficient lengths of time such that female preference can reach a high value before males attain their optimal investment strategy. This requires that the rate of male evolution is low relative to the rate of female evolution. Whether this will actually be the case depends on genetic details and on the intensity of selection on the male and female sexual characters.

Acknowledgments

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